

A CYTOTAXONOMIC STUDY OF THE  
HERBACEOUS SPECIES OF SMILAX:  
SECTION COPROSMANTHUS\*

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The herbaceous species of *Smilax* (section *Coprosmanthus*), widely distributed both in the Old and the New World, have their greatest concentration in the eastern half of the United States. The genus has been conventionally placed in the family Liliaceae. Ventenat isolated it from the Liliaceae and placed it under Smilaceae. Rafinesque removed the herbaceous species from *Smilax* on the basis of their non-prickly stems and the presence of staminodes in pistillate flowers, and placed them under a new genus *Nemexia*. Later, Torrey relegated these taxa to a new section, *Coprosmanthus* within the genus *Smilax*. Kunth, in turn, raised section *Coprosmanthus* to the level of genus. The naturalness of the new genus has often been questioned and most recent authors refer to the herbaceous species

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Voucher specimens and slides are deposited in the herbarium of The Catholic University of America.



under a section of *Smilax*. Small retained the genus name *Nemexia* in his Flora of the Southeastern United States and recognized eight species. Pennell, in his revision of the herbaceous species of *Smilax*, recognised nine species. Fernald, in Gray's Manual Ed. 8, and Gleason in Manual of Vascular Plants, recognised only three species and two varieties.

Thus, there is a diversity of views as to the number of species within this section and as to the circumscription of species and varieties. In many of the herbaria checked, misapplied names are often the rule rather than the exception. Moreover, no cytological work has been done within these taxa except for *Smilax herbacea*. The necessity of a revision is thus apparent.

The present study is an attempt to bring together all available information in order to clarify existing problems, especially at the specific level, with the hope that this synthesis may help to illuminate sectional relationships. Breeding experiments were not performed since seeds failed to germinate in culture. Acquaintances with local and regional populations, their habitats, and variability have been of extreme importance to the study.

Chromosomal information has been proved to be a significant aid, especially in elucidating the matter of dioecism in these taxa. Except for one taxon, chromosome numbers are uniform throughout section *Coprosmanthus*. I feel that many of the problems existing in this complex have been solved by this attempt.

The genus *Smilax* was proposed by Tournefort and later was included in Systema Naturae (1735) by Linnaeus. The genus included dioecious plants with flowers composed of six perianth parts, six stamens (more than six in the section *Pleiosmilax*), superior ovary of three carpels and 1-2 ovules in each locule.

Rafinesque (1825) circumscribed the herbaceous species with perennial rhizomes and annual herbaceous, non-prickly aerial shoots in a new genus, *Nemexia*. Torrey (1843) classified *Smilax herbacea* (*S. peduncularis*, *S. pulverulenta*



and *S. lasioneuron* were recognised as synonyms of *S. herbacea*) under the section *Coprosmanthus*, omitting the two other binomials, *S. pseudo-china* and *S. tamnifolia*, already published at that time. Kunth (1850) raised the section *Coprosmanthus* to the level of genus. De Candolle (1878) divided the genus *Smilax* into four sections, *Nemexia*, *Eusmilax*, *Coilanthus*, and *Pleiosmilax*, these being mainly based on the number of ovules, nature of perianth at anthesis and number of stamens. *Nemexia* was characterized by recurved perianth, six stamens, and biovulate carpels. However, *S. china* and its relatives, with woody stems and uniovulate carpels, were relegated to the section *Nemexia*. Koyama (1960) suggested that de Candolle included *S. china* under the section *Nemexia* thinking that the section is characterized by a single ovule to a locule but, in fact, de Candolle mentioned the biovulate locule in his description of the section: "*Flores musculi hexandri, sepalis petalisque plus minus excurvatis; feminei loculis biovulatis . . .*"

Most European authors, e.g., Bentham and Hooker (1883) and Krause (1930), followed de Candolle's system. However, most American authors have recognised two sections, *Eusmilax* and *Nemexia*, for the North American species. These sections generally divide the woody from the herbaceous taxa. Koyama (1960) divided *Smilax* (world wide basis) into six sections, *Pleiosmilax*, *Smilax*, *Macranthae*, *Coilanthus*, *China* and *Coprosmanthus*. The section *Coprosmanthus* is based mainly on the somewhat reflexed nature of the tepals at anthesis, presence of staminodes in pistillate flowers, and the fact that the petioles and blades fall off together. By rules of priority, *Coprosmanthus* is to be retained for the section that includes all the herbaceous species in the United States.

Linnaeus (1753) recognised two herbaceous species, *S. herbacea* and *S. pseudo-china*, from the North American Continent. Michaux (1803) added two more species, *S. pulverulenta* and *S. tamnifolia*. In the present paper, *S. tamnifolia* is recognised as a synonym of *S. pseudo-china*. Hooker (1840) added another species *S. lasioneuron*. Engel-



mann (1835) recognised a new variety, *S. herbacea* var. *ecirrhata*. However, the new varietal epithet was first validly published by Kunth (1850) as *Coprosmanthus herbaceus* var. *ecirratus*. Gray (1848) recognized two species and one variety in the section *Coprosmanthus*; Watson (1890) raised the variety *S. herbacea* var. *ecirrhata* to the rank of species in the 6th ed. of Gray's Manual.

Small (1898) circumscribed two new species, *S. tenuis* and *S. diversifolia*, but later (1903) he re-established the genus name *Nemexia* for the herbaceous species *Smilax* and recognised two more species, *N. hugeri* and *N. biltmoreana*. The taxonomic position of *S. tenuis* is not clear. Even though the stem and leaves are slender, it resembles *S. lasioneuron* in many respects and representative specimens are extremely rare in most herbaria checked. In the present treatment, *S. diversifolia* is included within *S. lasioneuron*. Pennell (1910) described a new variety, *S. herbacea* var. *crispifolia*, based on its relatively thick leaves, a character common among plants of this species growing in direct sunlight; in the present treatment, *S. herbacea* var. *crispifolia* is considered as an ecological variant. Pennell in 1916 attempted a taxonomic revision of the section and added one more species, *S. leptanthera*. This also, in the present treatment, is regarded as an ecological variant. Ahles (Radford, et. al. 1964) reduced *S. hugeri* and *S. biltmoreana* to two varieties of *S. ecirrhata*.

The section *Coprosmanthus* has a wide distribution on the eastern half of the North American Continent extending from the Gulf area to the Lake region and northward into Canada. In all eight species recognized, the annual shoots develop very early in the spring. Flower buds are already developed by the time the shoots emerge from the soil. The flowering period generally lasts about two weeks for each species; however, there is considerable variation within and between species with regard to the time of flowering. Most species flower between early May and late June. Therefore, a major part of the field work was done during these months



in 1963, 1964 and 1965. Representative specimens and cytological material were collected from Florida, South Carolina, North Carolina, Virginia, Maryland, Pennsylvania, Michigan, Illinois, and Wisconsin.

Most of the materials for cytological studies (especially flower buds) were collected in the field. The most favorable time of fixation was found to be between 11:30 A.M. and 12:30 P.M. Materials collected at other times showed practically no mitotic stages. In a few cases, however, good meiotic stages were obtained from flower buds collected early in the morning. Attempts were made to transplant rhizomes to the greenhouse. Shoots were cut back and the rhizomes were dug out and transplanted in pots and then transported to the greenhouse. Most specimens of *S. ecirrhata* complex, all with short erect shoots, survived while most specimens of *S. herbacea* complex, all with long climbing shoots, died in the greenhouse.

More than 20 random population samples of *Smilax herbacea* were collected from Virginia, Maryland, and Pennsylvania. A few population samples of *S. lasioneuron* and *S. pulverulenta* were also obtained. *Smilax hugeri*, *S. biltmoreana*, and *S. pseudo-china* were represented by widely spaced individuals rather than by populations. Therefore, only single specimens of these species could be acquired. Measurements were made mostly on herbarium specimens. Care was taken to select the specimens from wide geographic ranges. The list of herbaria consulted is provided elsewhere.

#### CHROMOSOMAL STUDIES

Because of the high morphological and ecological variability and wide distribution of the members of this section, it was thought early in the study that chromosomal information might be of considerable value in dealing with taxonomic problems. It soon became apparent that the number  $n = 13$  was constant for nearly all members of the section, the exception being *S. pseudo-china*.



*Methods:*

Root tip and flower bud squashes were used for chromosomal studies. Both materials were pre-treated with 0.002 mol/L solution of 8-hydroxyquinoline (ortho) and were fixed in modified Carnoy's fixative (4 chloroform: 3 absolute ethanol: 1 glacial acetic acid). The materials were kept in Carnoy's fixative for 24 hours and then preserved in 70% ethanol or were used immediately after thorough washing. Initial use of aceto-orcein and aceto-carmin procedures was abandoned since the meristematic cells became highly refractory and because certain granular bodies became as heavily stained as chromosomes.

A satisfactory staining procedure resulted from modifying Marimuthu and Subramaniam's (1960) hematoxylin squash technique. Both flower buds and root tips were hydrolysed in a mixture of concentrated HCl and absolute ethyl alcohol (1:1) for about one minute, then washed thoroughly in distilled water and mordanted in 2% ferric ammonium sulphate for about 5-10 minutes. The material was then washed in distilled water and stained in a time-ripened solution of hematoxylin for 10-15 minutes. (Other materials may require a longer staining period; overstaining is seldom a serious problem.) The tissue was softened and destained in 45% acetic acid at 60°C. for about one minute. Both hydrolysing and destaining time depend on the size and texture of the material. The material was then mounted in a drop of the same solution of 45% acetic acid and squashed under the coverslip. A quick survey of these temporary mounts was made, and good preparations were made permanent, using the CO<sub>2</sub> freeze technique, and mounted in green euparal. The chromosomes were stained dark blue with the background almost colorless.

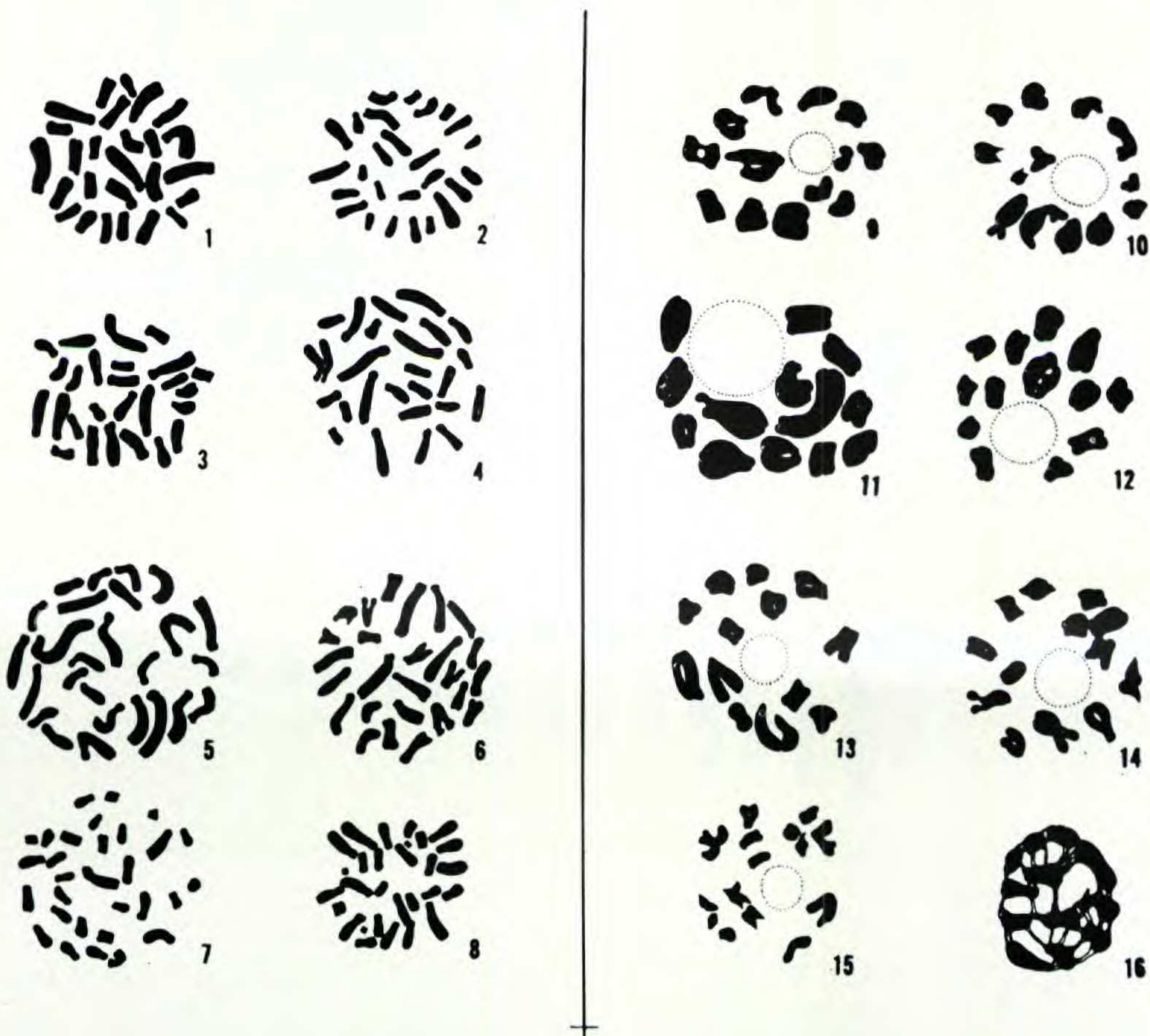
Drawings were made with the aid of a camera lucida. In some cases chromosomes were respaced to avoid overlapping.

*Results:*

Only one previous chromosomal count was reported for this section, *S. herbacea*,  $n = 13$  (Lindsay 1930). In the



following list, counts are recorded for plants of all 8 species comprising *Coprosmanthus*. All plants of the 8 species except those of *S. pseudo-china* have chromosome numbers  $2n = 26$  (Figs. 1-6 and 9-14). Two specimens of *S. pseudo-china*, both from South Carolina, have a chromosome number  $2n = 30$  (Figs. 7 and 15). Within karyotypes, chromosomes exhibit great variability with regard to their size and morphology. The longest chromosomes measure 6 microns



Figs. 1-8. Mitotic chromosomes of *Smilax* species.—1. *S. lasio-neuron*.—2. *S. herbacea*.—3. *S. illinoensis*.—4. *S. pulverulenta*.—5. *S. hugeri*.—6. *S. biltmoreana*.—7. *S. pseudo-china*.—8. an apparent hybrid of *S. biltmoreana* and *S. hugeri*, showing the extra chromosome fragments.

Figs. 9-16. Meiotic chromosomes of *Smilax* species.—9. *S. Lasio-neuron*.—10. *S. herbacea*.—11. *S. illinoensis*.—12. *S. pulverulenta*.—13. *S. hugeri*.—14. *S. biltmoreana*.—15. *S. pseudo-china*.—16. an apparent hybrid of *S. biltmoreana* and *S. hugeri* showing the lateral pairing of the bivalents.



while the shortest, 2 microns and there is gradation between these two extremes (Fig. 17). In all taxa, all chromosomes display subterminal centromeres. *S. pseudo-china* appears to have the smallest and *S. illinoensis* has the largest.

The plants of the genus *Smilax* are dioecious. Lindsay (1930) made an extensive study of the chromosomes of *S. herbacea* and reported the absence of any heteromorphic pair. On the other hand, she noticed at the periphery of the spindle an unusual pair of chromosomes with near terminal centromeres and practically free ends. From her figures, this chromosome pair appears to be one of the largest within the karyotype. She also suggested that the folding of the free end of a chromosome might result in the members of the pair appearing unequal in length. Such a case can only be verified when both the chromosomes of a homologous pair are seen in the profile view.

An attempt was made to determine the chromosomal basis of sex differentiation in this section. Microsporocytes of *Smilax* species here investigated disclose the presence of a

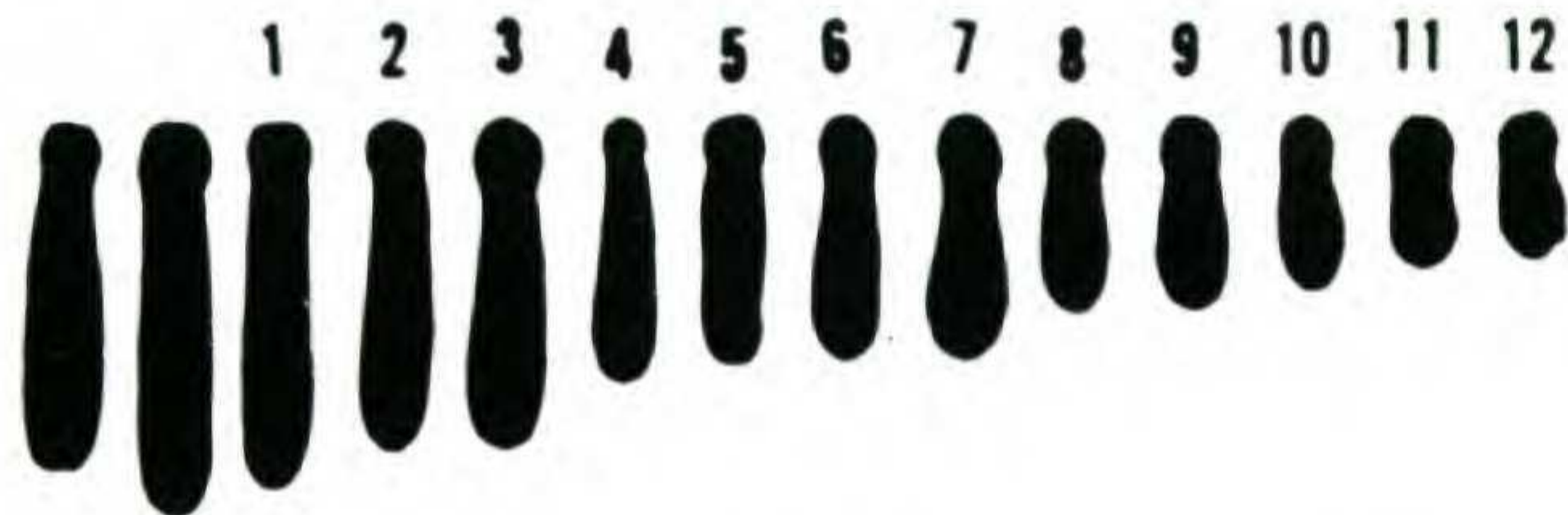


Fig. 17. Karyotype of *S. pulverulenta*. 1-12 somatic chromosomes, and the other two apparently sex chromosomes.

pair of unequal chromosomes during synapsis. This pair, one of the largest within the karyotype, is fairly distinct up to diakinesis (Figs. 9, 11, 12, and 13). Even at this stage the difference in size of the two chromosomes is not very prominent, and gradually it becomes indistinct during late prophase and metaphase as the chromosomes become further contracted. It is likely that this pair of unequal chromosomes with long free arms is the same that Lindsay observed in the periphery of the spindle. The presence of this heteromorphic pair during synapsis in microsporocytes suggests the possibility that the sex differentiation in *Smilax*, section



*Coprosmanthus*, is by X and Y chromosomes, where XX is female and XY is male. Such distinct heteromorphic pairs are noticed only in four species where very good stages of early prophase of the 1st meiotic divisions were obtained. In all other species this could not be verified. Therefore, at the present time this observation is far from conclusive.

Two specimens with perfect flowers were found in the herbarium materials checked. Both specimens were collected from Wisconsin. Attempts to collect bisexual living materials from their original localities were not successful. Therefore, no cytological investigation could be made.

#### CHROMOSOME NUMBERS

<i>Taxon</i>	<i>Coll. No.</i>	<i>County</i>	<i>Source</i>	<i>n</i> <i>PMC</i>	<i>2n</i> <i>Mi-</i> <i>tosis</i>
<i>Smilax</i>					
<i>herbacea</i>					
VIRGINIA					
	219		1.5 mi. south of Lewis Mt., Shenandoah National Park	—	26
	2135		Lewis Mountain, Shenandoah National Park	.. 13	26
	2137		4 mi. south of Lewis Mt., Shenandoah National Park	13	—
	2136		4 mi. south of Lewis Mt., Shenandoah National Park	13	—
PENNSYLVANIA					
	2002	Lycoming	Williamsport, Pa.	.. —	26
	2073	Clearfield	2 mi. south of Coal Hill on Route 219, Pa.	.. —	26
<i>S. lasioneuron</i>					
MICHIGAN					
	2145	Washtenaw	East of Delhi Rd., Delhi	—	26
ILLINOIS					
	2146	Cook	2 mi. west of Roselle on Route 72	.. .. —	26
	2147	Cook	2 mi. west of Roselle on Route 72	.. .. 13	26
	2148	Cook	2 mi. west of Roselle on Route 72	.. .. —	26



<i>Taxon</i>	<i>Coll. No.</i>	<i>County</i>	<i>Source</i>	<i>PMC</i>	<i>n</i>	<i>2n</i>	<i>Mitosis</i>
WISCONSIN							
	2152	Iowa	Jct. Rt. 18 and K, 1 mi. on K. . . . .	—			26
	2154	Iowa	Jct. Rt. 18 and K, 1 mi. on K. . . . .	—			26
	2163	Iowa	On Route 23 . . . . .	—			26
	2166	Iowa	Jct. Rt. 23 and Rt. 14	13			—
	2167	Iowa	Jct. Rt. 23 and Rt. 14	13			26
	2168	Iowa	Jct. Rt. 23 and Rt. 14	13			26
	2170	Iowa	Jct. Rt. 23 and Rt. 14	—			26
<i>S. pulverulenta</i>	VIRGINIA						
	206	Bath	Doutat State Park	—			26
	210	Allegheny	Strom, between Covington and Eagle Rock . . . . .	—			26
MARYLAND							
	231	Montgomery	Cabin John Park . . . . .	—			26
	2123	Montgomery	Cabin John Park . . . . .	13			26
	2124	Prince Georges	Laurel, Rt. 1, 15 mi. north of D.C. . . . .	—			26
	2126	Prince Georges	Laurel, Rt. 1, 15 mi. north of D.C. . . . .	13			26
	2127	Prince Georges	Laurel, Rt. 1, 15 mi. north of D.C. . . . .	—			26
<i>S. pseudo-china</i>	SOUTH CAROLINA						
	270	Sumter	6.8 mi. s.w. of Sumter on Route 15 . . . . .	—			30
	275	Orangeburg	2 mi. from Jct. Rt. 176 and 15, on Route 176 . . . . .	15			30
<i>S. illinoensis</i>	MICHIGAN						
	2143	Washtenaw	E. Delhi Road, Delhi . . . . .	13			26
	2144	Washtenaw	E. Delhi Road, Delhi . . . . .	—			26
<i>S. hugeri</i>	FLORIDA						
	282	Jackson	Marianna Caverns, Fla.	13			26



<i>Taxon</i>	<i>Coll. No.</i>	<i>County</i>	<i>Source</i>	<i>n</i> <i>PMC</i>	<i>2n</i> <i>tosis</i> <i>Mi-</i>
	285	Jackson	Marianna Caverns, Fla.	13	26
	291	Jackson	Marianna Caverns, Fla.	—	26
<i>S. biltmoreana</i>			FLORIDA		
	281	Jackson	Marianna Caverns, Fla.	13	—
	290	Jackson	Marianna Caverns, Fla.	—	26
	283	Jackson	Marianna Caverns, Fla.	—	26
<i>S. ecirrhata</i>			WISCONSIN		
	2180	Iowa	Jct. Rt. 23 and Rt. 14	—	26

#### CHROMOSOMAL ABERRATIONS IN THE SMILAX BILTMOREANA-S. HUGERI COMPLEX

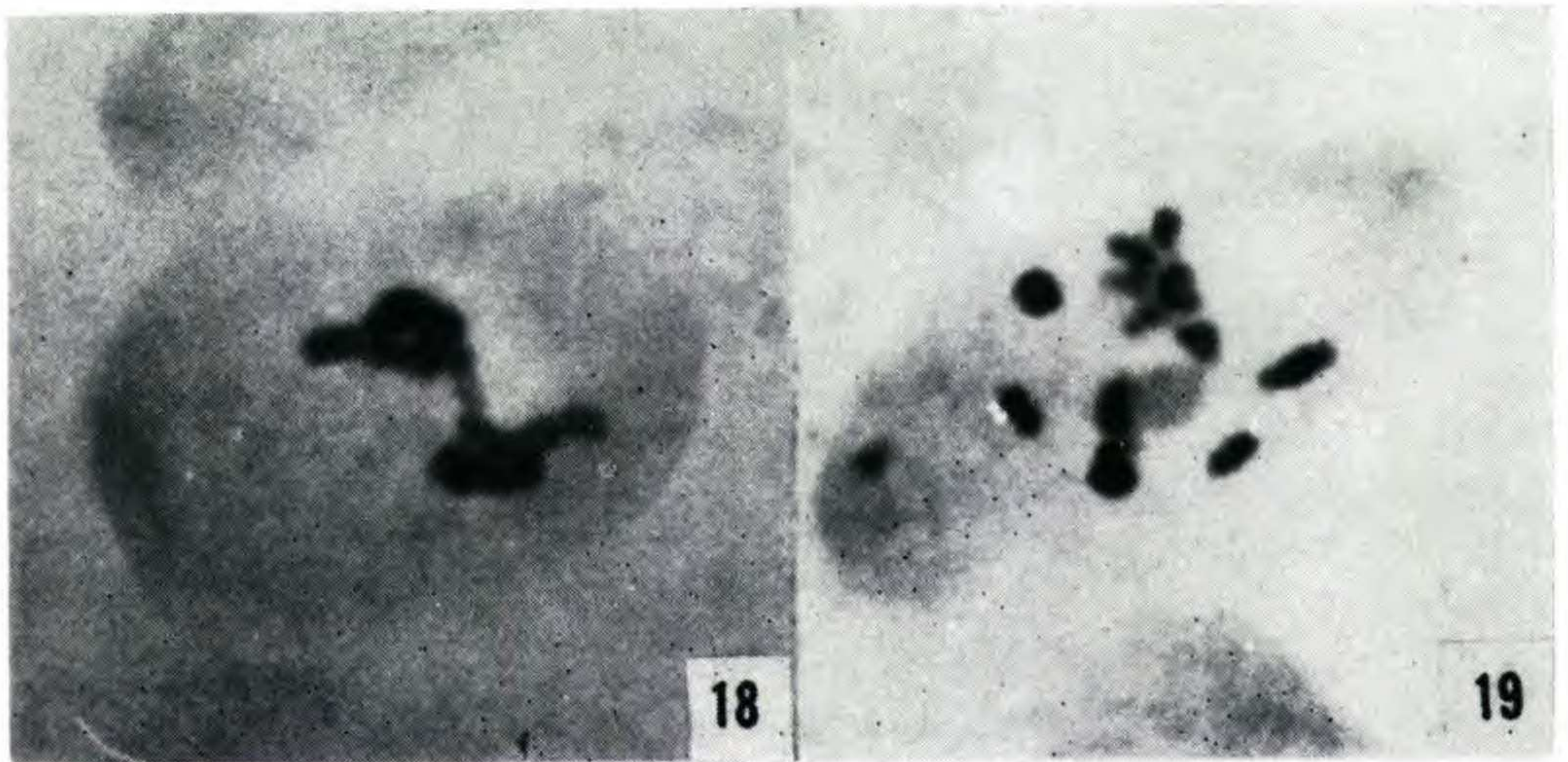
Exomorphologically intermediate forms of *Smilax biltmoreana* (Small) J. B. Norton and *S. hugeri* (Small) J. B. Norton are collected from undisturbed mixed woodland habitats near Marianna, Florida. Careful examination of herbarium specimens of these species indicates that populations from certain other localities are similarly confusing taxonomically. In these cases, misapplied names are the rule rather than the exception. This morphological evidence has suggested interspecific hybridization as a working hypothesis.

A total of fourteen plants from the Marianna population collected in the spring of 1964 was examined cytologically. Root tip and flower bud squashes were used for chromosomal studies. Both materials were fixed and stained as described previously. Nine of these were morphologically typical of the species. These plants exhibited a diploid chromosome-number of 26, and meiotic behavior was normal for the approximately 150 PMCs examined. However, three of the remaining five intermediate forms exhibited extra-chromosome fragments varying from two to eight, in addition to the normal chromosome complement (Fig. 8).

Abnormal meiotic pairing is conspicuous in intermediate forms. The synapsed chromosomes show lateral connections



## Plate 1372.



Figs. 18 and 19. Photomicrographs of pollen mother cells of *Smilax hugeri* — *S. biltmoreana* hybrids showing the unusual synaptic configurations. 18. thirteen bivalents in two small rings connected together. 19. the bivalents becoming free — six pairs still interconnected. (1200  $\times$ ).

between adjacent bivalents and without exception are arranged in rings or chains (Figs. 16, 18, and 19). Usually ten pairs form an outer ring with the other three remaining inside, interconnected. In most cells examined the later stages of meiotic divisions were apparently normal. Occasionally, however, lagging chromosomes were observed in anaphase. In anaphase I, the bivalents disengage and then continue normal anaphasic separation.

Examination of pollen under the microscope indicated that 35% of the pollen was shrivelled up in these plants which showed the cytological ring formation. Attempts were made to test pollen germination. Incubation at room temperature in 3% sucrose resulted in pollen tube formation in only 17% of 1000 grains examined.

The observed chromosomal aberrations in *Smilax* hybrids differ from the translocation systems in *Oenothera* and in *Rheo* by the presence of bivalent rings and chains. Although the available data are insufficient for a conclusive appraisal of the process they suggest that these aberrations result from a large number of reciprocal translocations of very



small units. Sterility of hybrids due to structural hybridity involving small chromosomal segments was suggested by Sax as early as 1933, for *Campsis chinensis* × *C. radicans*, and a large number of cases are known where hybrids show complete or partial sterility. The suggestion of Stebbins (1950) on the origin of translocations in connection with cryptic structural hybridity seems appropriate for *Smilax*. Equally important is the fact that when a translocation results in a deficiency in one chromosome, it also results in a duplication in another chromosome. If the chromosome complements of the hybrid parents have more translocated duplications than deletions it is likely that these hybrids might show more of structural aberrations at synapsis and less of sterility. (A manuscript with details of these observations has been submitted for publication.)

A few cytological problems remain unsolved. Two bisexual individuals collected from Wisconsin were found among the herbarium specimens. Attempts to collect such specimens in the spring of 1965 for cytological studies were not successful.

All species of this section except *S. pseudo-china* produce only one peduncle from a node. But some specimens of *S. pseudo-china*, especially from South Carolina and coastal Virginia, have three peduncles at the same node, a central long one and two shorter lateral ones. Whether there is a cytological basis for this atypical expression has not been determined.

#### MORPHOLOGIC AND TAXONOMIC CRITERIA

It is very difficult to evaluate morphological characters which are used taxonomically in this section, as most features are extremely variable in relation to ecological and climatic variations. This is particularly true in the case of the *S. herbacea* complex where the relative length of the peduncle and the leaf vary on the same plant. Also there is considerable variation in leaf shape between young and older plants. Consequently, taxonomic distinctions are mainly based on a combination of morphological features.



The characters listed below are useful principally in the determination of specific categories.

*Habit.* *Smilax ecirrhata* and associates are all small erect plants with no tendrils or with a few rudimentary ones. *Smilax illinoensis*, an intermediate form between *S. lasioneuron* and *S. ecirrhata*, is also erect and has a large number of tendrils mostly on the upper part of the stem. All others are fairly tall and climbing. All have perennial rhizomes with a few strong fibrous roots. The juvenile stage lasts about 3 - 6 years. Shoots from mature rhizomes of the *S. herbacea* complex often produce a few branches. Among older plants, more than one shoot usually appear from the same rhizome in one season.

*Leaves.* The shape of the leaf, number of veins, presence or absence of pubescence, character of tip and base, relative length of petiole and blade were used to differentiate species. The floral characters in this group are evolutionarily conservative and, therefore, vegetative characters like the morphology of the leaf have been used in delineating species even though such characters are ecologically plastic.

Leaf shape varies not only on different individuals of the same species, but on the same plant, depending on its location on the plant, and also among plants of different age. So extreme care should be taken to define species, with emphasis on the leaf shape. Another significant feature in the case of plants of the *S. herbacea* complex is that on older plants there is a gradual transition from scaly bracts at the base of the stem to the normal foliage leaves above. Pubescence and non-pubescence on the under-surface of the leaves of different species appear to be fairly constant. Of the three species with non-pubescent leaves, two grow mostly at higher elevations along the Appalachian Mountains and the third is restricted to the eastern Coastal Plain. Species with pubescent leaves extend to higher elevations too. This is especially true of *S. lasioneuron* which is dis-



tributed mostly in the central plains but is also found in the Great Smoky Mountain region and the eastern part of the Rockies.

*Inflorescence.* The inflorescence is a few to many flowered umbel. Its place of origin, whether axillary to bracts or not, is considered as an important taxonomic character for separation of species. The number of umbels and the number of flowers on each peduncle are also useful.

*Perianth.* The shape and the relative length and breadth of tepals are useful. In general, the inner ones are progressively narrower. Often the pistillate flowers have smaller tepals. In all species the tepals are light green and free.

*Stamens.* In most species the ratio of length of filament to that of anther is not uniform within the same flower, the outer ones with longer filaments and the inner ones slightly shorter. In general, however, relative length of anthers and filaments was found to be useful. In most species the anthers are shorter than the filaments; only in one are the anthers longer. These features are reliable only if the flowers are fully open.

*Fruits.* The fruit is a one-seeded to six-seeded berry. It is relatively uniform in shape, but color varies from blue to black among different species. The fruit wall is either glaucous or not. The number of seeds in a berry does not appear to be a species character even though the short *S. ecirrhata* complex has fewer seeds per fruit.

*Branching.* Only in the *S. herbacea* complex is branching prevalent and here the pattern of branching is almost the same in all species. Branches usually develop on the upper half of the stem. The leaves on the branches in general are smaller than those on the mature stem and vary more in shape. Thus, for most taxonomic purposes, only leaves on the stem were considered.



## FLOWERING

Preliminary investigations suggested that flowering in this section is not photoperiodically controlled. In early spring, when the annual shoots sprout, the flower buds develop along with them, even before the leaves fully expand. Thus, flowering begins before the shoot is exposed to any photoperiodic influence. As expected, the southern forms of a given species flower slightly earlier than the northern ones.

*Smilax hugeri* is the earliest to flower, beginning in early April and reaching its peak in the third week of April. *Smilax pseudo-china*, occurring sympatrically with *S. hugeri* in the Carolinas, reaches its peak flowering in May. *Smilax biltmoreana*, which occurs mostly in the mountains, has its peak flowering period during the second and third weeks of May. *Smilax pulverulenta* reaches its peak flowering in the second week of May and *S. lasioneuron*, with a farther northward distribution, has a peak flowering period from

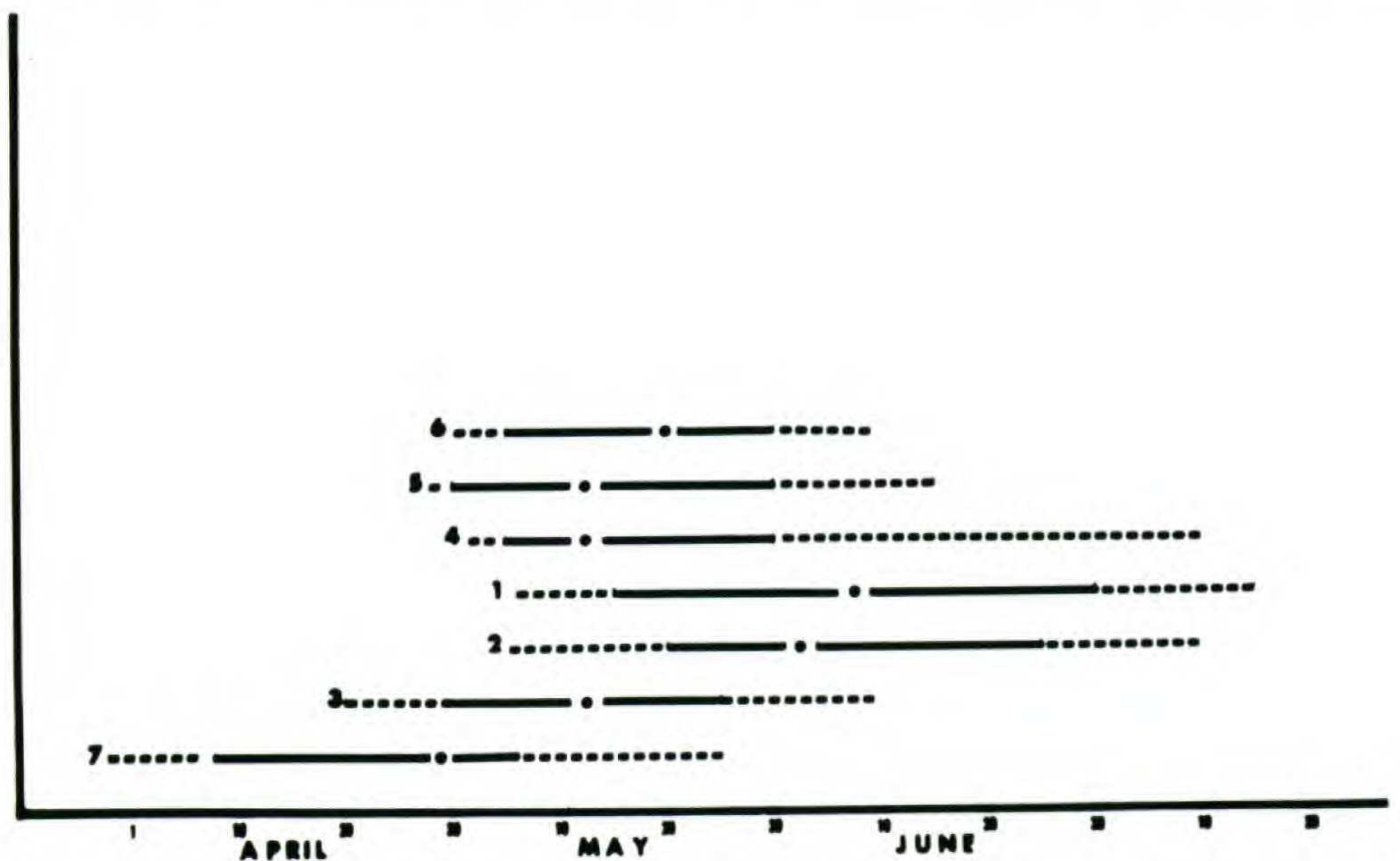


Fig. 20. Bar diagram showing the flowering interval in *Smilax* species: 1. *S. herbacea*. — 2. *S. lasioneuron*. — 3. *S. pulverulenta*. — 4. *S. pseudo-china*. — 5. *S. illinoensis*. — 6. *S. ecirrhata*. — 7. *S. hugeri*. The solid black line indicates the major interval of flowering and the dark spot in the middle represents the mode. The dotted lines show the interval in which flowering is irregular.



the third week of May in the Mid-central Plains to the second week of June in the northern parts. These two species have been recognised by some authors as two different varieties of *S. herbacea*. The difference in the flowering period between these two species might partly explain the rarity of intermediate forms as a result of partial or complete sexual isolation, even though both exist sympatrically in the Mid-central Plains.

*Smilax herbacea* reaches its peak flowering in the first week of June in the Carolinas and Virginia; it extends to the end of June in the New England States. *Smilax ecirrhata* and *S. illinoensis* reach their peak flowering in the third week of May, but *S. illinoensis* has a slightly more extended flowering period, ranging from the second week of May (Fig. 20).

#### POLLEN STUDIES

Pollen morphology is fairly uniform in the section. The exine is slightly spinous, 1 - 2 microns in thickness, and with no distinct furrow. Pollen size varies from 16.8 to 32.2 microns. *Smilax pseudo-china* has the smallest pollen with a mean size of 23.0 microns; the largest is that of *S. ecirrhata* with a mean value of 26.24 microns

Five plants were selected from each species and from each plant 50 pollen grains were measured at random. The mean value for each species was determined from these measurements. All together more than 2000 pollen grains from the eight species were measured.

<i>Species</i>	<i>Mean Size of Pollen</i>
<i>S. herbacea</i> . .	24.75 microns
<i>S. pulverulenta</i> . .	24.47 microns
<i>S. lasioneuron</i> . .	24.48 microns
<i>S. illinoensis</i> . .	25.54 microns
<i>S. ecirrhata</i> . .	26.24 microns
<i>S. hugeri</i> . .	24.44 microns
<i>S. pseudo-china</i> . .	23.00 microns

Pollen measurements are of particular interest in three species. The mean size of pollen in *S. lasioneuron* is 24.48



microns; in *S. ecirrhata*, 26.24 microns; in *S. illinoensis*, an apparent introgressant hybrid of the preceding two, 25.54 microns.

The morphology of the tendrils in *Smilax* has long been controversial. The tendrils have been homologised with many other plant organs; modified stipules; bipartite ligules, each tendril representing a demiligule; metamorphosed trichomes or emergences, and metamorphosed leaflets of a compound leaf. After extensive anatomical and morphological studies of the tendrils in *S. herbacea*, (Agnes) Arber (1920) demonstrated conclusively that these tendrils have arisen by chorsis or dedoublement of the petiole and so are equivalent to them. Working with *S. macrophylla*, Chakravarthi and Mitra (1948) have also reached the same conclusion that the tendrils are formed by chorsis or splitting of the petiole.

#### MEASUREMENTS OF MORPHOLOGICAL CHARACTERS

All measurements were made from dried herbarium specimens. In all cases, the largest leaf with its axillary peduncle, if any, was selected for measurement. The leaves on the branches were not used, as they differed from those on the main stem both in shape and size.

#### SPECIFIC CONCEPT

The section *Coprosmanthus* stands isolated from the woody sections by the presence of the annual herbaceous unarmed shoots arising from a perennial rhizome, and bi-ovulate carpels in contrast to the uniovulate carpels in the woody *Smilax*. Yet the differences between them are not sufficient enough to circumscribe them under two separate genera as suggested by Rafinesque (1825) and accepted by Small (1903), and so the author prefers to keep the herbaceous species under the section *Coprosmanthus* within the genus *Smilax*. The group as such has long been considered fairly distinct, the only problem being limited to the specific level. Observations of natural populations and greenhouse materials indicate that the shoots are highly sensitive to ecological variations, and show marked variation in ex-



ternal morphology, e.g., relative size of the leaves and peduncle, texture of leaves and height of the plant. In the presence of such ecological plasticity, it is likely that shoots developing from the same rhizome in different years might show morphological variation sufficient to result in the plants being considered as intraspecific categories. Therefore, prolonged observation under constant ecological conditions is necessary before attempting to designate such categories within species. No such intraspecific categories are recognised in this study.

#### GENERIC RELATIONSHIPS AND TAXONOMIC POSITION

The circumscription of the genus *Smilax* is generally accepted. The section *Coprosmanthus* represents a closely knit group of herbaceous species within the genus *Smilax*: smooth annual shoots from the perennial rhizomes; presence of staminodes on pistillate flowers; and the presence of biovulate carpels. The uniformity of the floral and vegetative characters is remarkable. The distinctions between the herbaceous and woody species are listed below:

<i>Herbaceous Smilax</i>	<i>Woody Smilax</i>
1. Shoots annual and herbaceous	Shoots perennial and woody
2. Stem smooth and unarmed	Stem armed (spinous)
3. Shoots short, erect, or up to 3 meters high and climbing	Shoots generally much taller and climbing
4. Peduncles in general long	Peduncles mostly short
5. Two ovules in each carpel	One ovule in each carpel

#### DISTRIBUTION, ECOLOGY AND EVOLUTION

The section *Coprosmanthus* has a wide distribution which extends throughout the eastern half of the North American Continent. All species prefer very moist, shady woods. *Smilax lasioneuron* thrives well even in dry soil. Most species prefer the plains. Only two species, *S. herbacea* and *S. biltmoreana*, have their distribution almost exclusively on mountains.

*Smilax pseudo-china* is restricted to the eastern Coastal Plain, extending from Georgia to New Jersey and southern New York. (Fig. 21). *Smilax herbacea*, like *S. biltmoreana*, prefers higher elevation and is reported as occurring



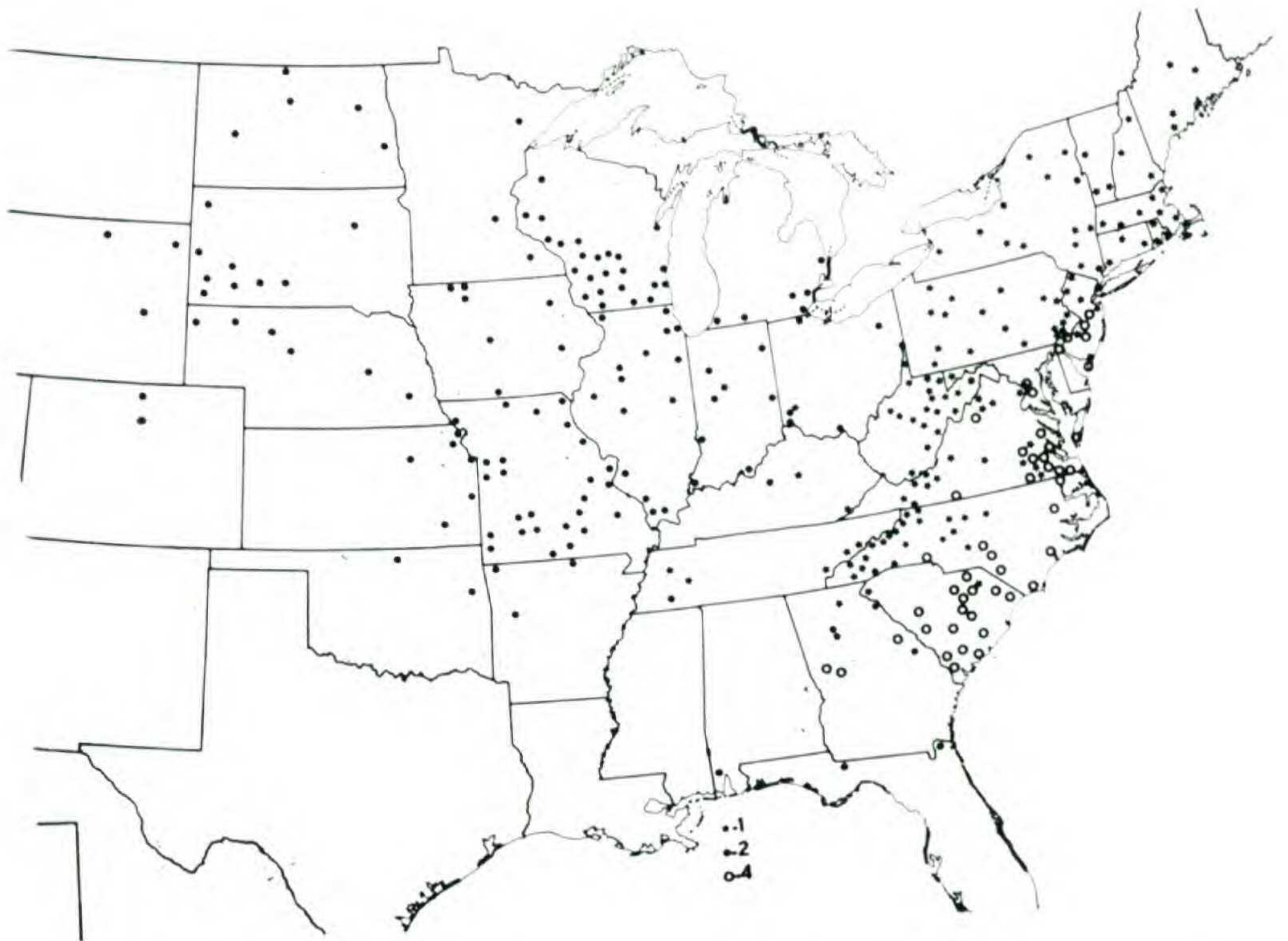


Fig. 21. Geographic distribution of *Smilax*: 1. *S. herbacea*. — 2. *S. lasioneuron*. — 4. *S. pseudo-china*.

only along the Appalachian and Blue Ridge Mountains. Thus its distribution extends from the Carolinas to the New England States and southeastern Canada (Fig. 21).

*Smilax biltmoreana* has a fairly restricted distribution. It is found in parts of North Carolina, South Carolina, Tennessee, Kentucky, Georgia, Alabama, and northern Florida (Fig. 23). *Smilax hugeri* has a more eastward distribution, extending to the Atlantic Coast. This species is also found in Tennessee and Kentucky (Fig. 22).

The distribution pattern of *Smilax pulverulenta* is rather unique. This species spreads across the Great Plains and reaches the Atlantic Coast through Virginia, Maryland, and New Jersey. It thus has a sympatric distribution with four other species of this section (Fig. 22).

*Smilax lasioneuron* is widely distributed throughout the Coastal Plains and northward into Canada (Fig. 21). The major distribution range of *S. ecirrhata* is the northern Central Plains (Fig. 23) and southern Canada.





Fig. 22. Geographic distribution of *Smilax*: 3. *S. pulverulenta*. — 5. *S. illinoensis*. — 7. *S. hugeri*.

*Smilax illinoensis* is distributed mostly in the Great Lakes Region, but it also extends to northern Missouri (Fig. 22). This species, a morphological intermediate between *S. lasioneuron* and *S. ecirrhata* and identified in most



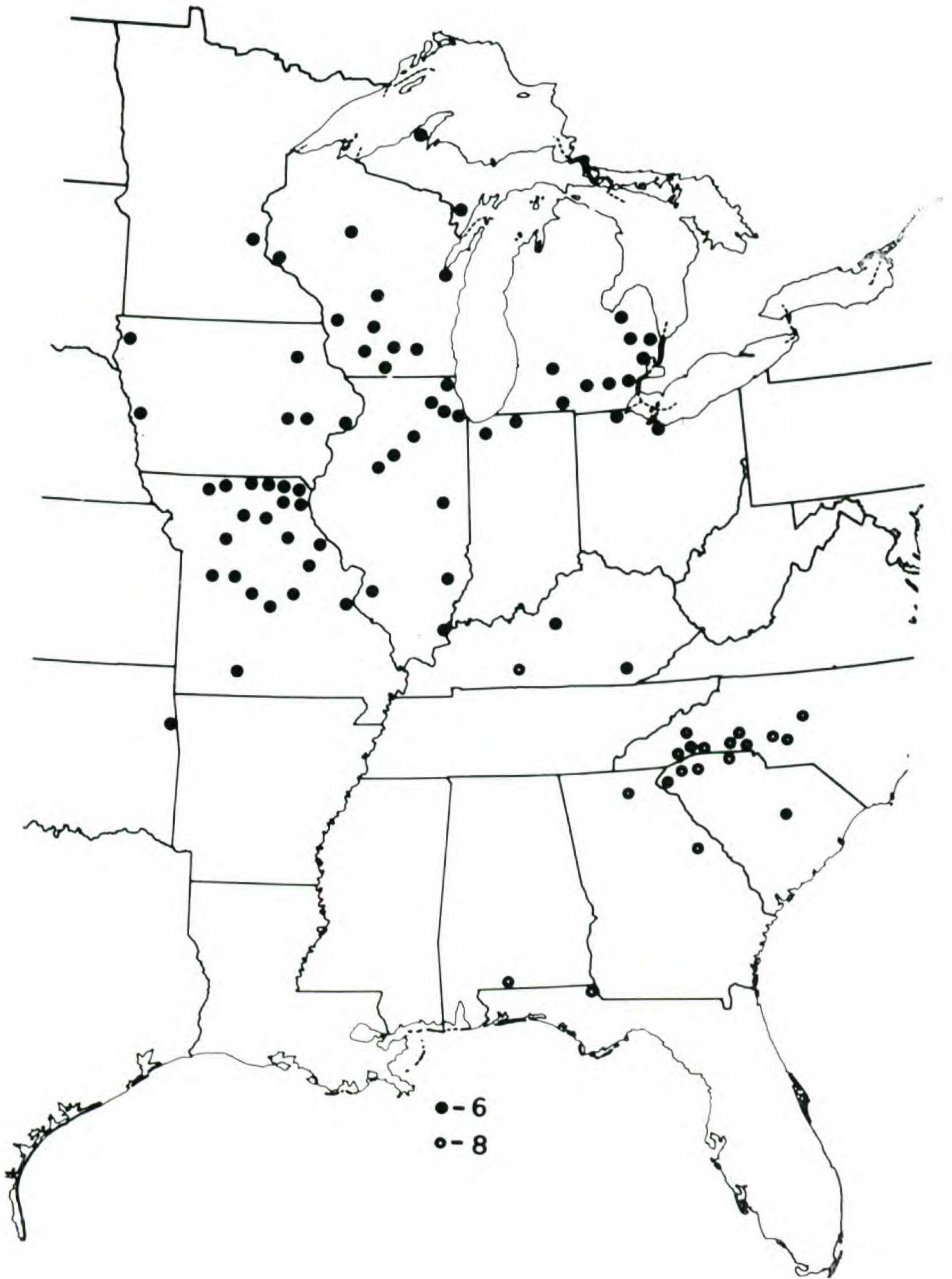
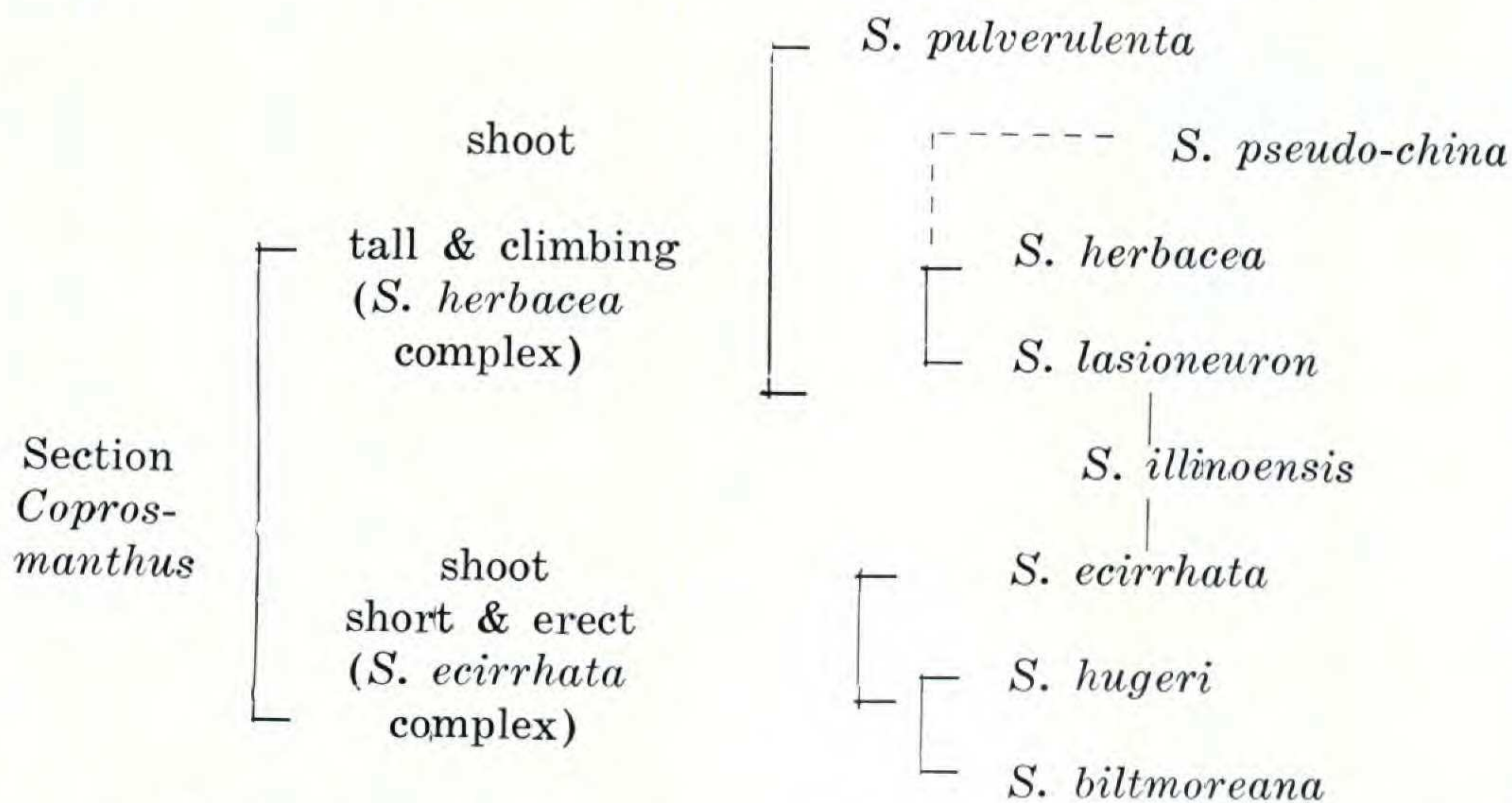


Fig. 23. Geographic distribution of *Smilax*: 6. *S. ecirrhata*.—8. *S. biltmoreana*.



herbaria as either of these two species or both, exists sympatrically with them. The greatest concentration of *S. illinoensis* is in Wisconsin, northern Illinois and Michigan and along the northern shores of the Great Lakes.



Both paleontology and comparative morphology strongly suggest the ancestral home of *Smilax*, both herbaceous and woody, to be in southeastern Asia, east of the Himalayas. The phylogeny of the section *Coprosmanthus* is not well understood. In eastern Asia, where the genus *Smilax* might have originated, the sectional barriers generally break down. Possibly, the Asian species *S. riparia*, widespread in Japan, Korea, and China, might give some insight into the probable ancestry of the section *Coprosmanthus*. Like all other herbaceous species, *S. riparia* produces annual shoots from the rhizome throughout Japan, Korea, and northern China, but in southern China the shoots are perennial.

Basing his conclusion on fossil evidence and comparative morphology, J. B. Norton (1916) traced both the eastward and westward migration route of *Smilax* from Asia to North America. He suggested that the herbaceous species of *Smilax* reached continental North America by an eastward migration along the path of *S. hispida*, by island hopping across the Pacific. These migrant ancestral forms might have been fairly well established in the central California region in Late Miocene or in Early Pliocene (Fig.



24). Any suggestion as to the establishment, further migration, and diversification of the group, in the absence of conclusive fossil evidence, remains purely hypothetical.

Fossil evidence of the vegetation both in Miocene and Mid-Pliocene indicate that in California both these epochs were comparatively dry and warm with a summer rainfall of 15 - 17 inches and the vegetation appears to have been similar to that of the present vegetation in this region. However, in the early Pliocene the climate was more or less equivalent to the present climate of eastern North America, and eastern Asia, with a minimum summer rainfall estimated to have been 25 - 30 inches (Axelrod, 1948). Such a moderate humid climate is ideal for *Smilax* and its presence in the California region during the Early Pliocene has been established by fossil evidence.

During the Middle Pliocene, when the climate became progressively warmer and drier, a general eastward migration might have occurred. Fossil evidence in western Kansas and Nebraska indicates clearly that the Middle Pliocene was the stage of greatest diversification of fossil types in contrast to the gradual changes in Miocene and Early Pliocene floras. Post Middle Pliocene was a time of large-scale mountain building, and as a result, a great diversification of the topography and habitat occurred. Added to that, the fluctuating Pleistocene climate kept the entire area in a continuous flux for a long time (Axelrod, 1948). This might have resulted in further diversification of the group that continues to the present time.

Whether the divergence of the section *Coprosmanthus* into the tall *Smilax herbacea* complex and the short *S. ecirrhata* complex was completed in Asia itself or the divergence occurred in continental North America is uncertain. This differentiation was probably distinct by the time the herbaceous species became established in Kansas and Nebraska during Late Pliocene. Probably at this time or even earlier, further diversification had already begun in the *S. herbacea* complex, with one branch providing the precursors of *S. pulverulenta* (Fig. 24). This new species



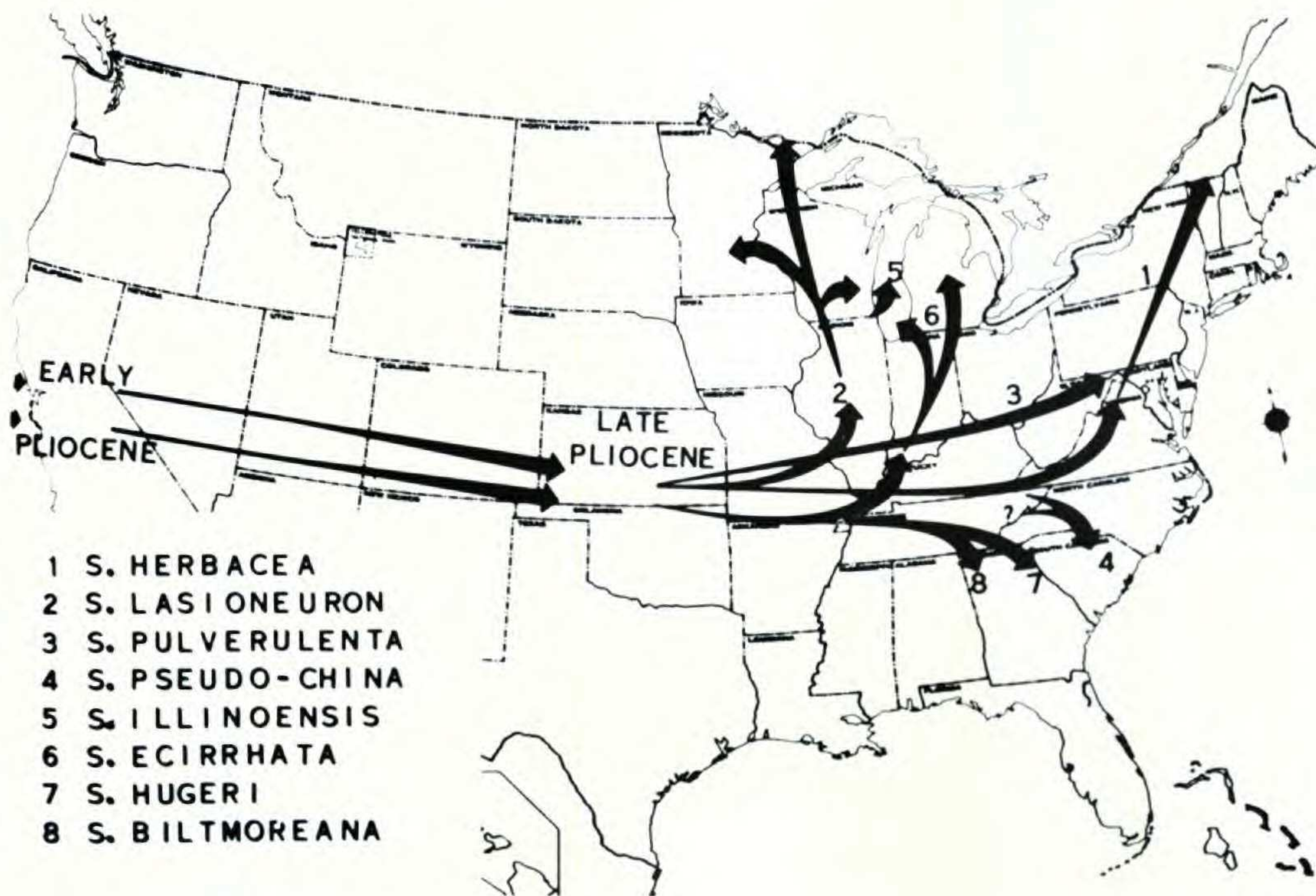


Fig. 24. Possible migration routes and diversification of herbaceous *Smilax* on Continental North America.

gradually spread further eastward and northward, eventually reaching the Atlantic Coast.

The other branch of *S. herbacea* complex also continued the general eastward migration and soon bifurcated. One branch, the ancestral forms of *S. lasioneuron*, spread mostly northward into Canada as the Pleistocene glaciers receded. The other branch, progenitor of *S. herbacea*, reached the Blue Ridge Mountains and spread northward all the way to eastern Canada along the Appalachian Mountains.

The phylogeny of *Smilax pseudo-china* is not clear. However, the morphological resemblance of this species to *S. herbacea* and the presence of higher chromosome numbers provide a working hypothesis that *S. pseudo-china* originated by interspecific hybridization of *S. herbacea* with some other *Smilax* species.

The other major group, the ancestral forms of *Smilax ecirrhata* complex, also first diverged into two groups. One branch, the fore-runners of *S. ecirrhata*, slowly spread northward in the same direction of *S. lasioneuron* and be-





Fig. 25. A. *Smilax illinoensis* and B. *Smilax ecirrhata*.



came established in the northern central plains towards the end of Pleistocene. Hybridization might have been fairly common between these two sympatric species. In suitable habitats around the Great Lakes, these hybrids, by further introgression, formed *S. illinoensis*.

The other branch of the *Smilax ecirrhata* complex continued to migrate eastwards into Tennessee and Kentucky and slowly diverged into two groups. One group, the progenitors of *S. biltmoreana*, spread along the mountains in Tennessee, Kentucky, the Carolinas, and Georgia. The other group migrated further eastward into the Carolinas and evolved into *S. hugeri*. In western Tennessee and Kentucky, the species differences of the *S. ecirrhata* complex are not as sharp as elsewhere, suggesting that the divergence of this complex probably occurred in this region.

Following is the list of herbaria from which specimens were borrowed during this study. The abbreviations used in citation of specimens are those recommended by Lanjouw and Stafleu (1963).

- Ann Arbor, Michigan; University Herbarium, University of Michigan (MICH)
- Athens, Georgia; Herbarium of the University of Georgia (GA)
- Austin, Texas; Herbarium of the University of Texas (TEX)
- Cambridge, Massachusetts; Arnold Arboretum of Harvard University (A)
- Cambridge, Massachusetts; Gray Herbarium of Harvard University (GH)
- Chapel Hill, North Carolina; Herbarium of University of North Carolina (NCU)
- Chicago, Illinois; Field Museum of Natural History (F)
- Gainesville, Florida; Herbarium, Agricultural Experiment Station (FLAS)
- Knoxville, Tennessee; Herbarium of the University of Tennessee (TENN)
- Laramie, Wyoming; Rocky Mountain Herbarium, University of Wyoming (RM)
- Madison, Wisconsin; Herbarium of the University of Wisconsin (WIS)
- Morgantown, West Virginia; Herbarium of West Virginia University (WVA)



New York, New York; New York Botanical Garden (NY)  
Philadelphia, Pennsylvania; University of Pennsylvania Herbarium  
(PENN)  
Philadelphia, Pennsylvania; Academy of Natural Sciences (PH)  
St. Louis, Missouri; Missouri Botanical Garden (MO)  
Tallahassee, Florida; Herbarium, Florida State University (FSU)  
Washington, D.C.; Herbarium, Catholic University of America (LCU)  
Washington, D.C.; National Museum, Smithsonian Institute (US)

TO BE CONTINUED